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Review of the systematic status of *Sceloporus arenicolus* Degenhardt and Jones, 1972 with an estimate of divergence time

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Abstract

The sagebrush lizards (*Sceloporus graciosus* group) consist of four taxa (*S. graciosus graciosus*, *S. graciosus gracilis*, *S. graciosus vandenburgianus*, and *S. arenicolus*) distributed in western North America. Of these, *S. arenicolus* is morphologically, behaviorally, and ecologically distinct as well as geographically disjunct from the other taxa, occurring only in the Mescalero-Monahans Sandhills of southeastern New Mexico and adjacent Texas. *Sceloporus arenicolus* is a taxon of concern because of its small range and habitat alteration due to land use practices. Understanding evolutionary relationships among members of the *S. graciosus* group, and especially *S. arenicolus*, has important implications for conservation. We examine the phylogenetic relationship of *S. arenicolus* relative to the three recognized subspecies of *S. graciosus* at mitochondrial and nuclear loci for populations sampled throughout the ranges of these taxa. Additionally, we estimate the divergence time and clade age of *S. arenicolus*. We find that the *S. graciosus* group is in need of major taxonomic revision, and also confirm that *S. arenicolus* is a genetically distinct and divergent lineage. These results bear important consequences for conservation and management.

Key words: *Sceloporus graciosus*, Mescalero-Monahans Sand Dunes, Phrynosomatidae, shinnery oak, evolutionarily significant unit (ESU), sagebrush lizard

Introduction

The sagebrush lizards are comprised of two species in the *graciosus* group of the phrynosomatid genus *Sceloporus* Wiegmann (1828)—*Sceloporus graciosus* Baird and Girard (1852) containing three subspecies *S. g. graciosus* Baird and Girard (1852), *S. g. gracilis* Baird and Girard (1852), and *S. g. vandenburgianus* Cope (1896) and *S. arenicolus* Degenhardt and Jones (1972). The taxonomy of this group has fluctuated considerably; *Sceloporus g. vandenburgianus* has previously been considered a distinct species from *S. graciosus* (Collins 1991), and likewise, *S. arenicolus* has previously been considered a geographical variant and subspecies of *S. graciosus* (Degenhardt & Jones 1972). As currently defined, *Sceloporus graciosus* occurs through most of the Great Basin of the western USA, to the coast of California, to northern Arizona and northwestern New Mexico (Figure 1; Stebbins 2003; Ryan 2009). The geographic range of *Sceloporus arenicolus* is disjunct from the ranges of the *S. graciosus* subspecies and occurs in southeastern New Mexico and adjacent Texas (Stebbins 2003; Fitzgerald & Painter 2009; Laurencio & Fitzgerald 2010).

The morphological and ecological distinctiveness of *S. arenicolus* from *S. graciosus* is well-studied. Specimens of *S. arenicolus* were originally identified by Sabath (1960), who reported it from Texas and New Mexico as a range extension of *S. graciosus* with distinct coloration patterns and femoral pore counts. Kerfoot (1968) conducted a comprehensive study of morphological variation among 1,311 specimens from throughout the eastern portion of the range of *S. graciosus* including the "southeastern sand dune isolates" which were populations

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of *S. arenicolus*, then considered *S. g. graciosu*s. Kerfoot's (1968) analyses identified *S. arenicolus* as a clear outlier from all other populations of *S. graciosus* based on distinct coloration and scalation of the body and head. Kerfoot (1968) noted, "Dorsal scale and midbody scale counts of these lizards [*S. arenicolus*] are unusually low, whereas the total number of femoral pores is unusually high." These populations were formally described as a subspecies*, S. g. arenicolus*, by Degenhardt and Jones (1972) based on morphology and coloration and Cole (1975) used karyotype data to confirm that *S. arenicolus* was more closely related to *S. graciosus* than *S. undulatus* (now *S. consobrinus*), a sympatric species. Based on the criterion of allopatry, Collins (1991) elevated three subspecies of the *S. graciosus* group (*S. g. arenicolus*, S. *g. graciosus, S. g. vandenburgianus*) to the level of species. Although this criterion was arbitrarily applied and a formal analysis was lacking, subsequent works have treated *S. arenicolus* as a valid species (Smith *et al*. 1992; Degenhardt *et al.* 1996; Fitzgerald & Painter 2009; Ryan 2009; deQuieroz & Reeder 2012).

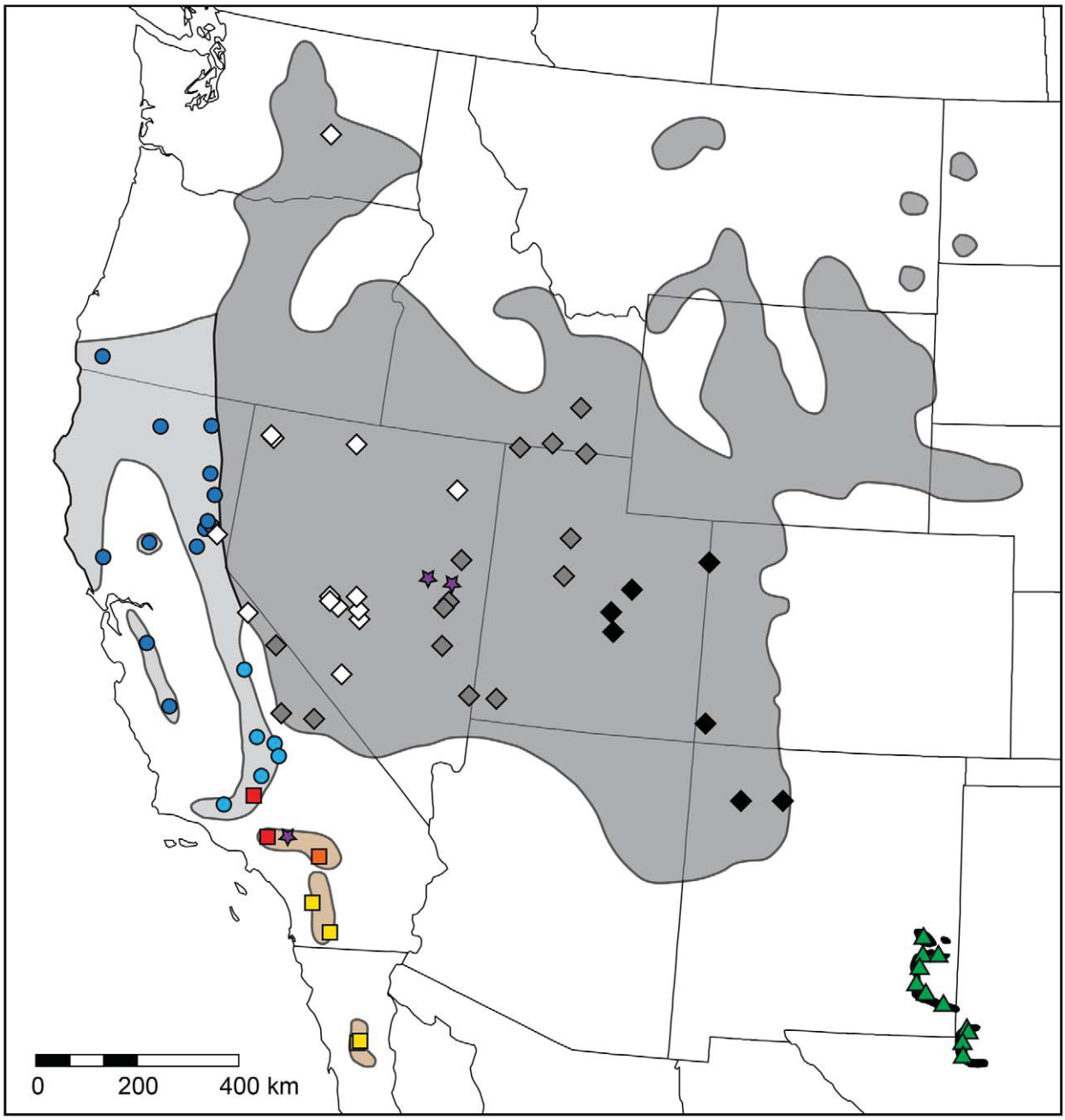

FIGURE 1. Collection localities for samples from the *Sceloporus graciosus* group included in this study. Colored symbols correspond to clade membership on Figure 3; three individuals for which we only have sequence data at *R35* are indicated with stars. Putative species and subspecies boundaries are shaded for the members of the *Sceloporus graciosus* group. *Sceloporus graciosus graciosus*: dark gray distribution, *S. g. gracilis*: light gray distribution, *S. g. vandenburgianus*: brown distribution, and *S. arenicolus*: black distribution.

Despite the apparent ecological and morphological distinctiveness of *S. arenicolus* and presumably long separation from other members of the *S. graciosus* group, the phylogenetic placement of *S. arenicolus* has mainly been explored within the context of broader systematic studies of the genus (Wiens & Reeder 1997; Leaché 2010; Wiens *et al*. 2010). A single study by Frabotta (2002) examined the mitochondrial relationships among populations from all members of the *S. graciosus* group and suggested that *S. arenicolus* evolved from within *S. graciosus*, though sampling from eastern *S. g. graciosus* and *S. arenicolus* was limited.

Further investigation of these proposed relationships with greater population level sampling throughout the geographic ranges of each group is warranted both for basic and applied reasons. Better understanding of the phylogenetic placement of *S. arenicolus* would clarify its relationships to other members of the *S. graciosus* group and give finer resolution to the clade within the phylogeny of *Sceloporus*. Additionally, clear understanding of the phylogenetic and taxonomic position of *S. arenicolus* bears important consequences for conservation. *Sceloporus arenicolus* is endemic to the Mescalero-Monahans Sandhills, a small and restricted ecosystem. Within this ecosystem *S. arenicolus* is an ecological specialist that only occurs in dunes stabilized by growing shinnery oak (*Quercus havardii*) that contain open sandy depressions (Fitzgerald & Painter 2009; Ryberg *et al*. 2012). Land use in the region has contributed to loss and fragmentation of shinnery dunes habitat, and the conservation status of the species is of growing concern to natural resource agencies, oil and gas interests, and landowners (Smolensky & Fitzgerald, 2010; 2011). *Sceloporus arenicolus* has been of concern to the US Fish and Wildlife Service since 1982, and it was proposed for listing as Endangered in December 2010 (U.S. Fish and Wildlife 2010). An understanding of the uniqueness, history, and divergence of *S. arenicolus* based on phylogenetic analyses will help inform and justify efforts to conserve it.

The phylogenetic relationships at the scale of species groups within the genus *Sceloporus* are well understood (Wiens & Reeder 1997; Leaché 2010; Wiens *et al*. 2010) and information also exists on population differentiation within *S. arenicolus* (Chan *et al*. 2009). As such, it is not our aim to re-evaluate deeper relationships within *Sceloporus*, nor finer-scale patterns of phylogenetic relationships within *S. arenicolus*. The purpose of this study is to use multilocus sequence data to clarify the phylogenetic relationship of *S. arenicolus* relative to populations of *S. graciosus*. In addition, we estimate the clade age of extant *S. arenicolus* and the divergence time from its most recent common ancestor (MRCA) to evaluate the evolutionary history of this group. This work will enhance our understanding of relationships in the *S. graciosus* group as well as provide the first comprehensive phylogenetic analysis of the group that clarifies the position of *S. arenicolus*.

Methods

Sampling and molecular genetic data collection. Tissues samples for *S. graciosus* and *S. arenicolus* were obtained from vouchered specimens in museum and personal collections and from individuals captured in the field (toe and tail preserved in 95% EtOH) (Appendix 1). Whole genomic DNA was extracted from liver samples and tail and toe clips using the DNeasy Blood and Tissue Kit (Qiagen). Five protein-coding gene regions were targeted for sequencing using PCR amplification. These included two mitochondrial regions, NADH dehydrogenase 1 (*ND1*) with the primers tMet and 16dR (Leaché & Reeder 2002) and cytochrome-b (*cyt-b*) using the primers L14724 and H15915 (Irwin *et al*. 1991), in addition to three nuclear regions, the pinin gene (*PNN*), recombination activating gene-1 (*RAG1*), and RNA fingerprint protein 35 (*R35*) (primers from Leaché 2010).

PCR was done in 15 µl reactions with 1 x Buffer, 2.0 mM $MgCl_2$, 0.33 mM each dNTP (0.53 mM for *RAG1*), 0.4-0.6 µM each primer, and 0.375 U (mtDNA), 0.5 U (*R35* and *PNN*), or 0.75 U (*RAG1*) *Taq* polymerase (Sigma JumpStart). Reactions for *RAG1* and *PNN* additionally included 1% DMSO. Amplification cycles consisted of an initial denaturation step at 94°C for 3 minutes followed by 35 cycles (40 for *RAG1*) of 94°C for 1 min (30 sec for nuclear genes), locus specific annealing temperature (54°C *ND1*, 45°C *cyt-b*, 52°C *RAG1*, 58°C *R35* and *PNN*) for 1 min (30 sec for nuclear genes) and a 72°C extension for 90 sec. Cycles were followed by a final extension of 72°C for 10 min.

PCR product was cleaned with 0.5 µL of ExoSapIT (USB) and sequenced in $1/16^{th}$ reactions using the same primers used for amplification. Sequence data were collected on an ABI 3730xl. Chromatograms were assembled and checked for errors in Geneious 5.6 (Biomatters). We included sequence data from both mitochondrial genes for three phrynosomatid relatives (*Urosaurus, Uta,* and *Phrynosoma*) and three *Sceloporus* species (*S. jarrovii, S.*

merriami, and *S. occidentalis*) representing major clades in the analyses of Leaché (2010) (Appendix 2). We used the MAFFT plug-in in Geneious to align sequences for each gene region. Alignments were adjusted by hand and checked to ensure the absence of premature stop-codons; new sequences were deposited in GenBank (KC853767 – KC854153). For each nuclear locus, we constructed parsimony haplotype networks in TCS 1.2 (Clement *et al*. 2000) using a connection limit of 95%.

Phylogenetic reconstruction. Phylogenetic analyses were conducted on the concatenated mitochondrial DNA dataset under both Bayesian and Maximum Likelihood (ML) statistical frameworks. Redundant mitochondrial haplotypes were omitted from the alignment prior to analysis to reduce computational time. We used DT-ModSel (Minin *et al*. 2003) to determine the best-fit model of DNA sequence evolution for each codon position of each gene. Partitioned Bayesian phylogenetic analyses were conducted in MrBayes 3.2.1 (Ronquist & Huelsenbeck 2003). Two independent final runs each consisted of a single chain run sampled every 1,000 generations for 25 million generations. We confirmed adequate mixing within runs and convergence between runs in Tracer 1.5 (Rambaut & Drummond 2007) and summarized the final 75% posterior distribution of trees on the half-compatible consensus phylogeny. One-hundred partitioned ML bootstrap replicates were conducted in Garli 2.0 (Zwickl 2006). Each bootstrap replicate consisted of five independent search replicates with search termination thresholds of 5,000 generations and 0.001 LnL units. Bootstrap scores were summarized on the consensus phylogeny from the Bayesian phylogenetic analysis using the SumTree script from the DendroPy package (Sukumaran & Holder 2010).

Divergence time estimation. We additionally estimated the mitochondrial divergence times among all individuals sampled from the *S. graciosus* group in BEAST 1.7.5 (Drummond & Rambaut 2007). We assumed uncorrelated relaxed lognormal clocks for separate *ND1* and *cyt-b* partitions each with normally distributed prior substitution rates (mean of 1.5% per myr, standard deviation of 0.5% myr). This brackets mitochondrial substitution rates reported for other iguanian lizards (Bryson *et al*. 2011; Chan *et al*. 2012). We conducted analyses under a Yule speciation tree model. Replicate analyses were conducted to ensure adequate mixing and convergence and the final run consisted of 50 million generations sampled every 5,000 generations. We summarized the clade ages after discarding the first 10% of samples as burnin.

Results

We recovered the entire coding region of *ND1* (990 base pairs, bp) for 85 individuals from the *S. graciosus* group and partial *cyt-b* sequences (1128 bp) for 81 individuals. Of the 2,118 bp of mtDNA, 748 sites were variable and 617 were parsimony informative. Nuclear regions were much less variable: for 930 bp of *PNN* for 64 individuals, nine sites were variable and four were parsimony informative. Eighty-eight individuals sequenced for *R35* had 658 bp; of these 25 were variable and 11 were parsimony informative. Finally, we recovered 1,046 bp for *RAG1* from 70 individuals of which 14 of 29 variable sites were parsimony informative.

Haplotype networks for the nuclear loci showed that common haplotypes were shared among members of the *S. graciosus* group (Figure 2). *Sceloporus arenicolus* had unique alleles at all three loci, but shared a common allele with all subspecies of *S. graciosus* at PNN and with *S. g. graciosus* at RAG1.

We partitioned the mtDNA sequence data by gene and codon position for phylogenetic analyses. For *cyt b*, an HKY+I+Γ model was applied to first and second codon positions, and a TrN+ Γ model was applied to the third position. For *ND1*, TVM+ Γ, HKY+I, and TIM+I+ Γ were applied to first, second, and third codon positions, respectively. Bayesian and ML analyses were highly concordant (Figure 3). We found strong support for the monophyly of the *S. graciosus* group as well as the monophyly of *S. arenicolus* (PP=1, Bootstrap = 100). None of the other putative taxa (*S. g. graciosus, S. g. gracilis*, and *S. g. vandenburgianus*) were supported as monophyletic.

Divergence time analyses assuming a mean substitution rate of 1.5% per mya estimated the mean root age of the *S. graciosus* group to be 9.21 million years (Ma) with a 95% highest posterior density (HPD) of 5.70 – 13.91 Ma. The mean divergence time between *S. arenicolus* and the MRCA was 2.55 Ma (95% HPD: 1.43 – 3.93 Ma) while the mean clade age of *S. arenicolus* was 0.66 Ma (95% HPD: 0.34 – 1.06 Ma).

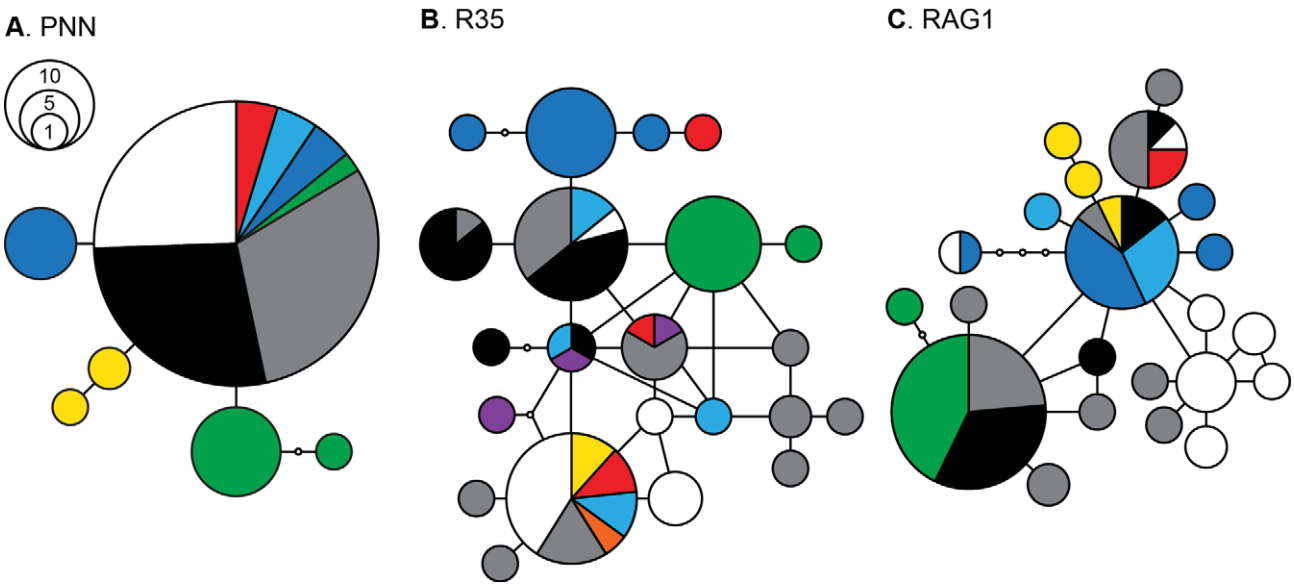

FIGURE 2. Minimum spanning haplotype networks for all *S. graciosus* group samples sequenced at each of three nuclear loci. Size of each circle corresponds to the frequency of that haplotype. Shading corresponds to clade membership in Figure 3.

Discussion

Consistent with previous studies focusing on broader systematic relationships (Wiens & Reeder 1997; Leaché 2010; Wiens *et al*. 2010), we find strong support for a monophyletic *S. graciosus* group. We additionally find unequivocal support for the monophyly of *S. arenicolus* at mtDNA loci. In contrast, *S. g. graciosus, S. g. gracilis,* and *S. g. vandenburgianus* are each recovered as paraphyletic or polyphyletic indicating that the *S. graciosus* group as a whole requires major taxonomic revision. The only other phylogenetic study of the *S. graciosus* group to include population sampling to date (Frabotta 2002) suggested that *S. arenicolus* fell within *S. g. graciosus*. That study had limited samples of eastern *S. g. graciosus* and in this study we were able to incorporate numerous samples from the eastern range of *S. g. graciosus* including samples from the populations in closest proximity to *S. arenicolus*. As such, our results corroborate and enhance previous work with greater genetic and geographic sampling. In both Bayesian and ML phylogenetic reconstruction of mitochondrial sequence data, *S. arenicolus* falls within a well-supported clade of eastern *S. g. graciosus* (Figure 3). Low nucleotide diversity at nuclear loci prevents phylogenetic reconstruction, but haplotype networks show that *S. arenicolus* does share haplotypes with other described taxa at two of the three nuclear gene regions examined (Figure 2). In both instances, *S. arenicolus* shares a single common haplotype at that locus and all other nuclear alleles found among *S. arenicolus* are unique to that group. Shared alleles at these two protein-coding nuclear loci are consistent with the general expectations of slowly evolving nuclear genes given recent divergence of *S. arenicolus* from within the *S. graciosus* group, in particular populations in the southeastern portion of the distribution of *S. g. graciosus*.

Our phylogenetic results corroborate discussion of *S. gracious* group systematics by Wiens and Reeder (1997) stating that "*Sceloporus arenicolus* is clearly allopatric and diagnosable, whereas *S. vandenburgianus* may be distinct but is morphologically similar and geographically close to *S. graciosus* (Censky 1986)." The morphological distinctiveness of *S. arenicolus* is well-known (Sabath 1960; Kerfoot 1968; Degenhardt & Jones 1972) and it is specialized, both ecologically and behaviorally, to live in the shinnery oak dune system where it is endemic. Based on a mean substitution rate of 1.5% per mya and a relaxed molecular clock, we estimate that divergence of *S. arenicolus* from its MRCA occurred approximately 2.55 Ma and extant populations coalesce to about 0.66 Ma. Thus, *S. arenicolus* has long been isolated from other members of the *S. graciosus* group. Given that it is geographically disjunct and locally endemic, it is likely this taxon is an example of divergence through peripheral isolation.

Our results show *S. arenicolus* is a unique evolutionary lineage that is genetically distinct, in addition to being ecologically, morphologically, and geographically distinct. We find complex relationships among the currently delineated subspecies of *S. graciosus* with clades largely consisting of geographic clusters with no support for the

monophyly of any subspecies. This indicates the need for taxonomic reassessment and revision of this group and while such revisions are beyond the scope of this current study, we suggest that any taxonomic revisions take into account the species-level distinctiveness of *S. arenicolus*, despite its rendering *S. graciosus* paraphyletic (Kizirian & Donnelly 2004; Rieppel 2010).

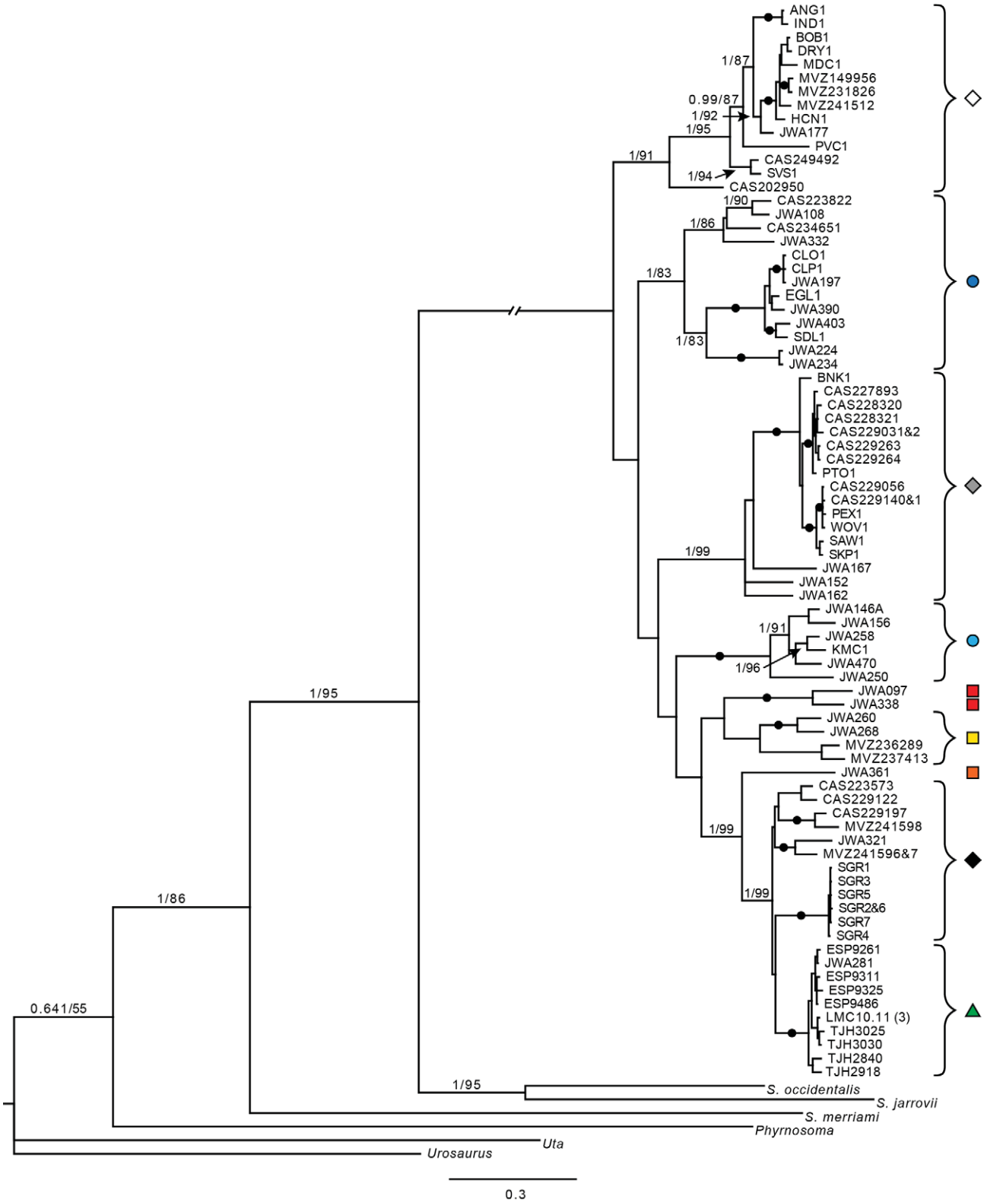

FIGURE 3. Consensus tree from Bayesian phylogenetic analysis. Bayesian posterior probabilities (PP) and ML bootstrap support (BS) are noted at nodes with high support (> 95% PP and 75 BS) and at basal nodes. Nodal support of PP = 1 and BS = 100 are indicated with a solid circle at the branch. Shaded symbols correspond to collection localities on Figure 1.

Conservation of *S. arenicolus* begins with proper identification of *S. arenicolus* and a stable taxonomy (Morrison *et al*. 2009). The recent proposal by the U. S. Fish and Wildlife Service to list *S. arenicolus* as federally endangered led to public commentary and confusion among stakeholder groups about the accurate taxonomic identity of *S. arenicolus* as a species (U.S. Fish & Wildlife Service 2010; 2012). As such, this study was partly motivated to provide a clear and stabilizing answer that would inform policy and conservation interventions (May 1990; Funk *et al*. 2002). The phylogenetic evidence presented here demonstrates *S. arenicolus* constitutes a long-isolated, monophyletic lineage easily distinguished from all other populations of *S. graciosus*.

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